

SHORT COMMUNICATIONS

Observations of within-colony breeding synchrony in Jackass Penguins.—The Jackass Penguin (*Spheniscus demersus*) is a colonial seabird breeding year-round on the southern tip of the African continent. A west coast, winter breeding peak (May–September) has been found to occur, corresponding to peak food availability, lowered ambient temperatures, and maximum chick survival (Cooper 1980, Wilson 1985). At St. Croix Island on the east coast, it has been suggested that egg-laying peaks by Jackass Penguins show greater synchrony within colonies than over the island as a whole (Randall and Randall 1981). Synchrony of egg laying is believed to occur in breeding groups of Galapagos (*Spheniscus mendiculus*) (Boersma 1976) and crested (*Eudyptes*) penguins (Warham 1975). To date however, no data have been presented on the degree of synchrony between separate penguin colonies at a single breeding locality. This paper reports the occurrence of breeding synchrony in the Jackass Penguin at the colony level.

Methods.—We investigated breeding synchrony of Jackass Penguins nesting on Dassen Island (33°25'S, 18°16'E) situated off the west coast of South Africa. Between June and August 1989, we determined the date of brood initiation (hatching of first chick) for all nests in three low-density colonies. Low-density colonies were defined as areas accessible from the sea by a common landing point, and containing nests spaced 1–11 m apart. Birds within these areas are in sufficiently close proximity to experience regular social interactions. Daily checks of nests allowed us to determine the day of hatching (chick clear of the egg shell). The length of our field season prevented us from obtaining information on overall breeding success or dates of clutch initiation. We also counted nests in eight high-density colonies over one week in mid-July 1989. A high-density colony was defined as an aggregation of nests with inter-nest distances of approximately 1 m (Hockey and Hallinan 1981), with a minimum of 200 m separating adjacent colonies. Nests were typically shallow burrows within a common area of between 118 and 216 m². Inter-nest distances were measured as a straight line between nearest neighbors. Colony area was measured as a rectangle encompassing all measured nests. At each colony the contents of nests were categorized into one of three stages, each representing approximately six weeks of the offspring's dependent phase: (1) eggs (0–6 weeks; assuming all eggs are fertile), (2) downy chicks (6–12 weeks); and (3) down-droppers and fully feathered chicks (12–18 weeks), assuming a mean incubation period of six weeks (38 days, Williams and Cooper 1984), mean time from hatching to fledging 12 weeks (80 days, Williams and Cooper 1984), and a mean time from hatching until the development of true feathers six weeks (Table 1).

One of us (J.C.) counted numbers of active nests in eight distinct colonies at 10-day to one-month intervals during November 1971 to October 1972 at Dassen Island. Colonies

TABLE 1
LENGTH IN DAYS (MEAN \pm SD, AND RANGE) OF THE BREEDING STAGES OF THE JACKASS PENGUIN

	Incubation	Hatch to down drop	Hatch to fledge
This study	—	44 \pm 3 (40–50)	85 \pm 9.2 (74–113)
Williams and Cooper (1984)	38 \pm 0.8 (37–39)	—	80 \pm 7.0 (65–90)

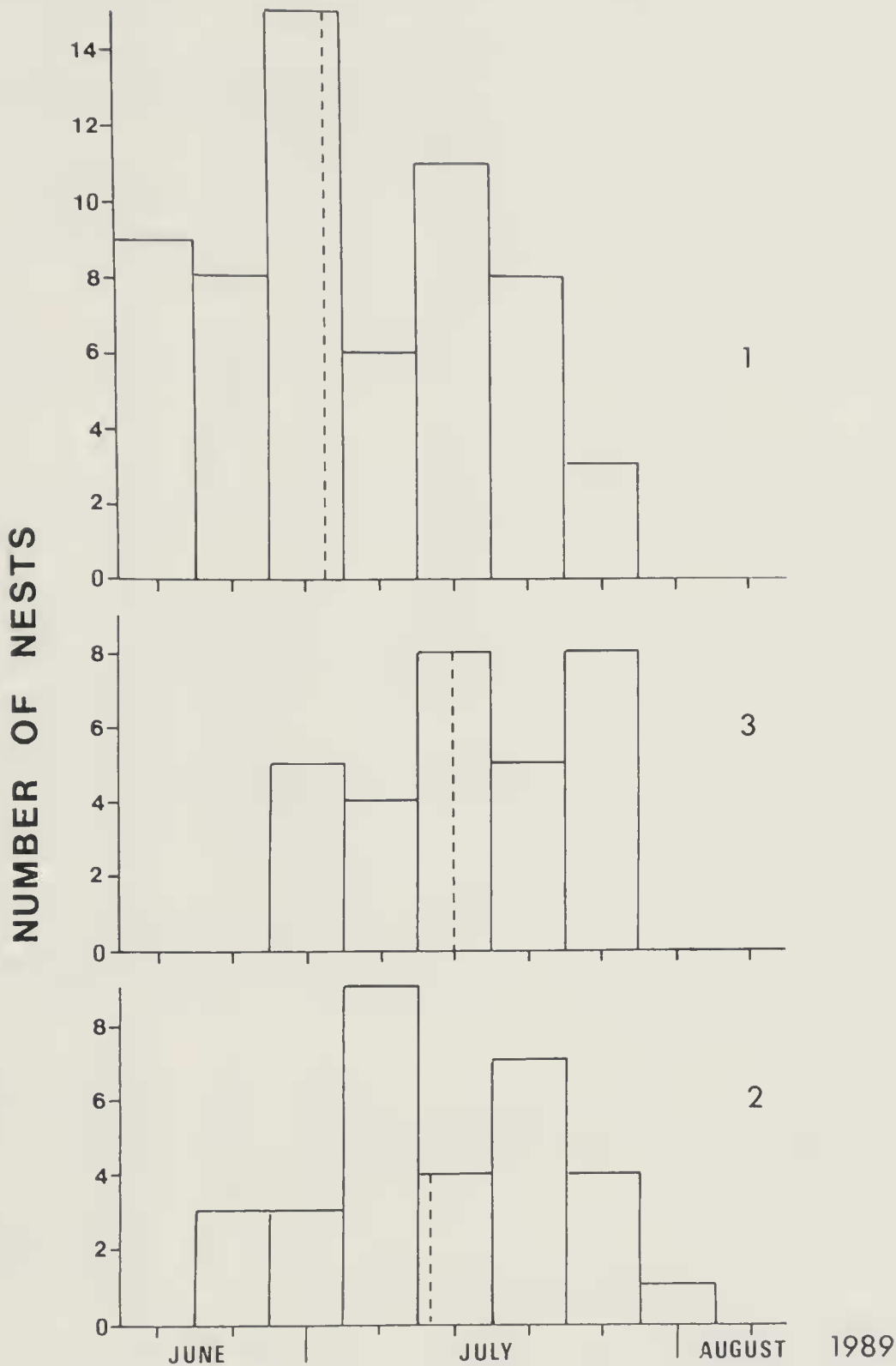


FIG. 1. Timing of chick-hatching in three low-density colonies of Jackass Penguins. Dotted lines indicate first 90% means.

were situated over the whole island, with no less than 100 m separating adjacent areas. At each visit the following were recorded: (1) the total number of active nest sites, i.e., nests containing eggs or chicks; (2) the number of nests containing a full clutch of two eggs; (3) the number of nests containing one or two small-downy chicks. Small-downy chicks were defined as chicks between one and 15 days old, and were characterized by their covering of sparse primary down. A census of active nests in discrete areas over a 12-month period allows the separation of localized breeding peaks from any general seasonal peaks.

Results.—There were peaks in the number of broods initiated in the three low-density colonies, with some clumping of hatching evident (Fig. 1). Means calculated from the first

TABLE 2
RANGES AND STANDARD DEVIATIONS OF BROOD INITIATION DATES IN THREE LOW-DENSITY JACKASS PENGUIN COLONIES

Area	Number of nests	Span (days)					Standard deviation				
		First (%)			Mid (%)		First (%)			Mid (%)	
		100	90	50	90	50	100	90	50	90	50
1	62	39	33	17	33	19	10.3	9.1	5.5	9.0	5.3
2	32	40	30	19	28	14	9.6	8.3	5.8	8.0	5.1
3	30	26	23	12	23	14	8.0	7.1	3.9	7.2	4.4

90% of broods initiated show small between-colony differences suggestive of within-colony synchrony (Fig. 1). There was a significant difference in the timing of hatching between the three colonies (Kruskal-Wallis test statistic 18.02, $df = 2$, $P < 0.0001$). Hatching ranged over 26–40 days (Table 2). Similarities between first and mid-90% hatching ranges in all three areas indicate close intra-area mean and median values and, therefore approximately normal distributions (Table 2). However, differences between first and mid-50% spans of hatching in areas 1 and 3 suggest distributions skewed slightly to the left, and hence a tendency towards early egg laying (Table 2). First and mid-standard deviations indicate comparable degrees of synchrony in all three areas (Table 2).

Seven of the eight high-density colonies showed a significant bias in the proportions of stages represented (Table 3). The bias was not in a consistent direction between colonies; of the eight areas, four had mainly eggs, one had downy chicks, and down-droppers/feathered chicks predominated in three.

Proportions of nests containing two eggs in the eight colonies surveyed over 12 months show a seasonal peak around November, with a possible second peak between May and June. The precise placement of the two peaks differed between colonies (Fig. 2), ranging from early November to early January and from early June to late August. Some areas show a single peak seemingly independent of seasonal effects (e.g., area 4 peaks in early May). The occurrence of small downy chicks in nests reflects the two-egg peaks but shows more clearly the differences between areas with first peaks ranging from early November to late February and secondary peaks between May and August.

Discussion.—Although showing some clumping, hatching in low-density colonies was not highly synchronized. Variation within these colonies may have been due to sub-colony effects, with small denser aggregations of nests showing greater synchrony. Peaks in hatching were similar between the three low-density study colonies, and insufficient in themselves, due to the lack of data from earlier and later months, to distinguish between the passive synchronizing effect of a possible seasonal breeding peak and local-scale synchrony due to social stimulation.

Hailman (1964) examined synchrony in gulls by recording the proportions of birds at each breeding stage. This method allows a researcher to make approximate statements about synchrony based on brief visits and is satisfactory for comparisons among colonies of a single place or species (Gochfeld 1980). A synchronous colony would have most birds at one particular stage, while a less synchronous colony may have equal proportions at each stage. This type of census is particularly suited to Jackass Penguins, which may breed at any time during the year, so that any stage of breeding may be represented at any time.

TABLE 3
COUNTS OF BREEDING STAGES IN HIGH-DENSITY JACKASS PENGUIN COLONIES

Colony	Eggs	Downy young	Feathered young	Total
1	3	22	[24]	49**
2	16	10	[23]	49 NS
3	[14]	11	2	27*
4	8	13	[36]	57**
5	[30]	4	4	38**
6	[29]	7	3	39**
7	[31]	6	6	43**
8	5	[24]	5	34**

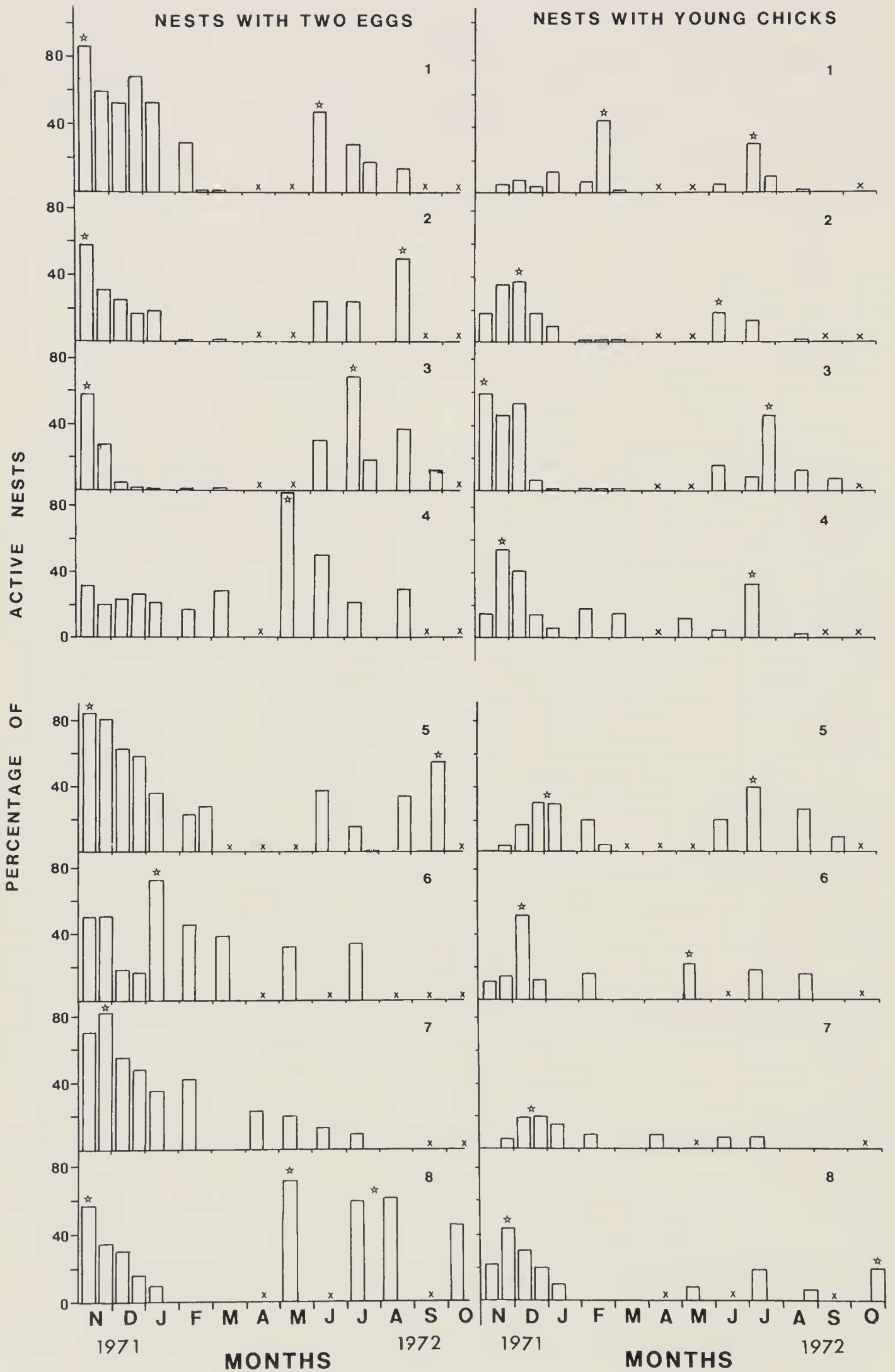
^a [] = predominant stage; NS = not significant; * $P < 0.05$; ** $P < 0.01$ (Chi-square one-sample test).

Two possibilities are apparent when considering the relative proportions of the different stages of breeding represented in the high-density colonies surveyed in 1989: (1) If we assume that there is no breeding peak, we would expect to find birds at all stages of breeding, and in any given colony all stages would be represented equally. This was not so, with seven of the eight colonies sampled showing a significant bias in stages; and (2) If the bias were simply a result of an overall breeding peak, we would expect that the bias in stages would be in a consistent direction and that every colony would reflect the overall frequency of stages. However, we found that the bias was not toward a single stage and that each of the three identified stages predominated in one or more of the study colonies.

Further support for the existence of local synchronizing events comes from the 12-month census data. If we assume that only a seasonal effect exists to produce synchrony, with birds breeding in an optimal "window" of time, we would expect that each colony would show a flattened (platykurtic) distribution of numbers of breeding birds and that the placement of the plateau of the frequency curve would not differ between areas. If local synchrony occurs within the breeding peak, the frequency distribution of breeding birds would be more peaked (leptokurtic). Most birds should breed within the peak time, but the precise location of the breeding peak will vary between areas. The wider the range of peaks between areas, the greater the evidence for local synchrony rather than just a general seasonal effect. Our results show that even when counting proportions of nests with full clutches or downy chicks, rather than the more precise dates of clutch initiation or hatching, a considerable inter-colony variation in the placement of breeding peaks was evident. The total absence of active nests during some census periods throughout the year and the subsequent rapid build-up in breeding numbers confirms the existence of synchronizing factors working at the colony level.

Breeding in a particular colony may become more synchronous if social facilitation of visual displays such as mutual ecstatic, bowing, or copulatory behaviour (Eggleton and Siegfried 1979) occurs. Copulation is socially facilitated in the Adelic penguin (*Pygoscelis adeliae*) (L. S. Davis, pers. comm.). Even in the absence of direct visual contact, vocal displays, too, may cause an increase in the frequency of sexual behavior by conspecifics. Acoustic displays in Little Blue Penguins (*Eudyptula minor*) have been shown to increase the rate at which perceiving conspecifics copulate and perform courtship displays (Waas 1988).

Spatial and temporal clustering of breeding may produce benefits for participating birds apart from those relating to optimal foraging conditions. Enhanced success for peak-breeding



birds may be due to such factors as improved incubation, decreased desertion (Spurr 1977), reduced predation through predator satiation (Darling 1938) or group aggressive defense (for review see Gochfeld 1980).

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FIG. 2. Percentage of nests containing: (a) a full clutch of two eggs, and (b) one or two small downy chicks, in eight Jackass Penguin colonies over a 12-month period (November 1971–October 1972). Stars indicate breeding peaks.